

NOTES ON THE BIOLOGY, HOSTS, AND IMMATURE STAGES OF
TOMOPLAGIA CRESSONI ACZÉL IN SOUTHERN CALIFORNIA
(DIPTERA: TEPHRITIDAE)

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Abstract.—*Tomoplagia cressoni* Aczél is oligophagous in flower heads of *Perezia microcephala* (deCandolle) Gray and *Trixis californica* Kellogg (Asteraceae) in southern California. Both hosts are in the tribe Mutiseae. Third instar larvae and puparia, and two new types of sensilla on them, are described for the first time. The larvae feed on the floral tubes and ovules as first and second instars, respectively, but most growth occurs in the third instar. The third instar feeds mainly on sap that collects in a cup-shaped cavity it chews in the receptacle. Most seeds in infested heads were undamaged. Mating behavior is described, which is unique among non-frugivorous Tephritidae for the more posterior, upright position of the male and the back and forth, rhythmic movements of his abdomen during initial phases of copulation. The unusual “butterfly stroke” wing movements of adults when walking also are described. This tephritid has a spring generation on *Tr. californica*, a summer generation on *P. microcephala*, and facultatively, a fall generation, again on *Tr. californica*, depending on the incidence of late-summer, desert rainfall triggering a second flowering.

Eurytoma veronia Bugbee (Eurytomidae), *Colotrechnus ignotus* Burks (Pteromalidae), and *Pteromalus* sp. (Pteromalidae) are reported as primary, solitary, hymenopterous parasitoids of *To. cressoni*.

Key Words: Insecta, *Tomoplagia*, *Perezia*, *Trixis*, life history, parasitoids, sensilla

This paper concerns the rare, stenophagous, previously little-known species, *Tomoplagia cressoni* Aczél, which does not lend itself readily to field or laboratory study. *To. cressoni* Aczél is the only representative of its genus in California (Foote and Blanc 1963); one of only two species of *Tomoplagia* known from North American north of Mexico; and one of 43 known species in this genus, most of which are restricted to tropical and subtropical America (Aczél 1955). Our admittedly incomplete findings on *To. cressoni* provide a base of knowledge of its biology, hosts, and immature stages.

TAXONOMY

Aczél (1955) first described *To. cressoni* and partly illustrated the adults with simple drawings and a photograph of a wing. Foote and Blanc (1963) also provided a wing photograph.

Larvae and puparia excised from flower heads of *Perezia microcephala* (deCandolle) Gray (Asteraceae) were examined with scanning electron microscopy (SEM) by DHH. Materials, methods, and nomenclature were as used by Headrick and Goeden (1990a) and Goeden and Headrick (1990). Means \pm SE are used throughout this paper.

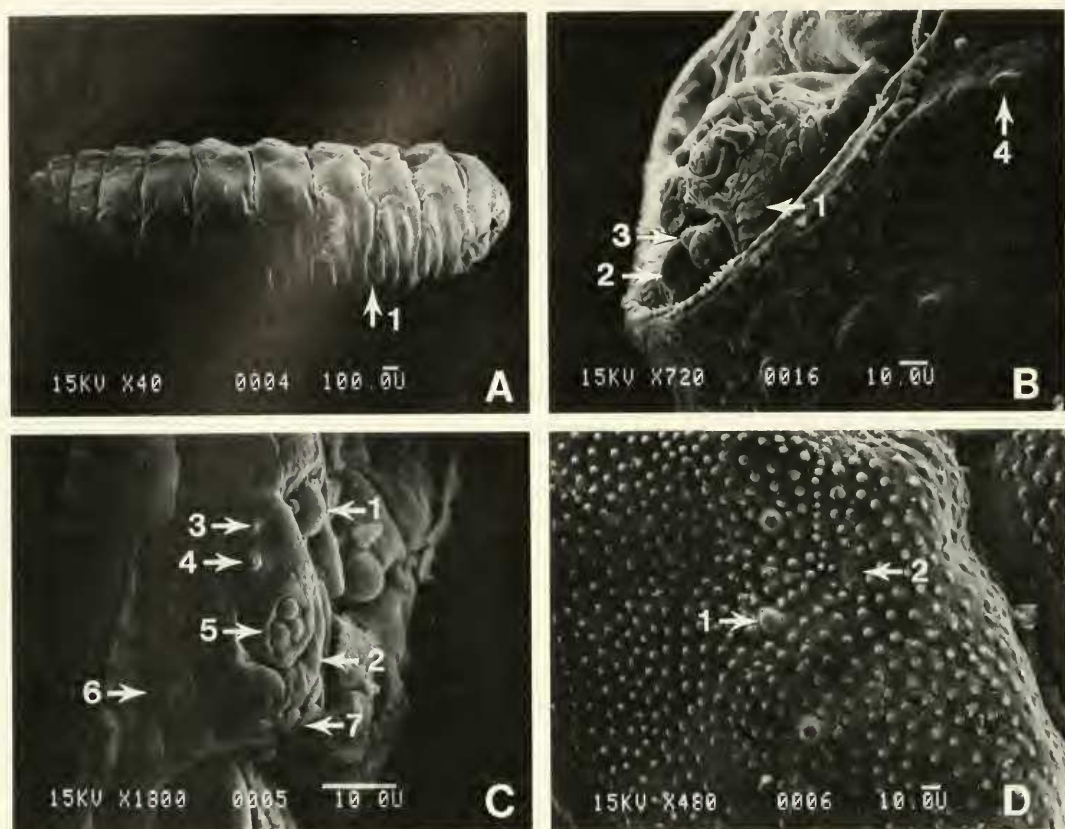


Fig. 1. Third instar larva, *Tomoplagia cressoni*. A. Habitus; 1—ventral transverse folds. B. Anterior end; 1—rugose pads; 2—mouthhooks; 3—median oral lobe; 4—thoracic sensillum. C. Anterior sensory organs; 1—dorsal sensory organ; 2—anterior sensory lobe; 3—sensillum; 4—lateral sensory organ; 5—terminal sensory organ; 6—lateral sensory lobe; 7—integumental petals. D. Abdominal segment, lateral view; 1—sensillum; 2—spiracle scar.

Third instar larva.—Four larvae were used for SEM. The mature larva of *To. cressoni* has a distinct habitus (Fig. 1A); it is more elongate and not barrel-shaped like other non-frugivorous, tephritid larvae thus far examined. The larva has deeply furrowed segmental lines, which circumscribed its body, and transverse folds ventrally on each segment (Fig. 1A-1). The integument in life is yellowish and shagreened; this texture is caused by evenly distributed, smooth, domed-shaped verrucae, seen with SEM.

The gnathocephalon is rounded and bears many rugose pads. The pads laterad to the mouth lumen are serrated on their ventral

edge (Fig. 1B-1). The paired dorsal sensory organs are composed of a single, spherical papilla (Fig. 1C-1). Ventrad and slightly laterad to the dorsal sensory organs are the paired anterior sensory lobes (Fig. 1C-2). The relative position of these sensory organs is atypical among the tephritid larvae examined to date. Headrick and Goeden (1990a) noted that placement of the sensory organs among non-frugivorous tephritid larvae is relatively constant. Most often, the dorsal sensory organ is dorsad to the anterior sensory lobe along a dorso-ventral line that is parallel with the midline of the body (cf., *Paracantha gentilis*, Headrick and Goe-

den 1990a). However, in *To. cressoni* the dorso-ventro axis of the anterior sensory lobes is directed slightly laterad of the midline, and the dorsal sensory organs lay mediad to the anterior sensory lobes and slightly closer to the mouth lumen.

The anterior lobes appear to bear three sensory organs; however, the pit sensory organ is not visible on the specimen used for Fig. 1C. A papillate sensillum is located dorsally on the anterior lobe (Fig. 1C-3), and may represent an aberration, as this sensillum type and placement has not been observed on any other tephritid larvae examined to date (Headrick, unpublished data). Both the lateral sensory organ and the terminal sensory organ are typical in placement and form (Fig. 1C-4, -5).

The lateral lobes are located dorso-lateral to the mouth lumen and bear several sensilla (Fig. 1C-6). The mouth lumen is surrounded by integumental petals (Fig. 1C-7) that are not as reduced as those of *Tephritis baccharis* (Coquillett) (Goeden and Headrick, submitted) nor as developed as those of *Paracantha gentilis* Hering (Headrick and Goeden 1990a). The mouthhooks have one large, curved, bluntly tapered tooth distally (Fig. 1B-2), and basally a smaller, more stout tooth on the lateral edge (not shown in Fig. 1B). The median oral lobe is laterally flattened, and has a rounded apex and a smooth ventral edge (Fig. 1B-3).

The integument of the thoracic segment is roughened with rows of flattened verrucae and dotted with larger papillate sensilla, each with a central pore (Fig. 1B-4). The anterior thoracic spiracles each bear three tubular spiracular openings (see puparium Fig. 3B).

The succeeding segments have both their anterior and posterior edges marked with rows of bluntly pointed acanthae. The integument is shagreened with small, evenly distributed, dome-shaped verrucae. Laterally, each abdominal segment bears a vertical row of three dome-shaped sensilla, each with a central pore (Fig. 1D-1). Also on each abdominal segment, and anterior to the row

of sensilla is a small ecdysial scar which is the vestige of the lateral abdominal spiracle (Fig. 1D-2). The tracheae of this spiracle can be seen within the puparium after adult emergence (cf., Headrick and Goeden 1990a).

The caudal segment has the typical four-dorsal, six-ventral arrangement of sensilla around its posterior margin (Fig. 2A). These sensilla are composed of two distinct morphological types. The first type is a basal crown of six points, from which projects a finger-like process. This type of sensillum is morphologically distinct from other sensilla reported in the Tephritidae thus far, and accordingly, we termed it a "stelex" sensillum (Fig. 2B). There are dorsal and ventral pairs of these sensilla located just laterad of the dorso-ventral midline (Fig. 2A-1). The other more common type is a domed sensillum with a central papilla (Fig. 2C). Three pairs of domed sensilla located laterally on the posterior margin complete a ring of 10 sensilla (Fig. 2A-2). A pair of previously undescribed sensory organs lie dorsad of the posterior spiracles on either side of the dorso-ventral midline (Fig. 2A-3). This sensory organ is smooth, dome-shaped, and bears two sensilla (Fig. 2D), a dorsal stelex sensillum and a ventro-lateral smaller dome with a cluster of finger-like filaments, which we term a "medusoid" sensillum (Fig. 2E). This sensillum superficially resembles the coniform sensillar complexes found on the antennae of the nymph of the stonefly, *Paragnetina media* (Walker) (Kapoor 1986), and the styloconic sensillum on the antenna of the adult of *Glossina austeni* Newstead (Lewis 1970). However, the terminal filaments of the *T. cressoni* sensillum appear to be free from each other in life, and not attached as in the stonefly nymph and *Glossina* adult. Thus, we do not include this sensillum in the coniform sensillar group until transmission electron microscopy studies can confirm similar nervous innervation and a porous substructure to each of the filaments; features which are fundamental to

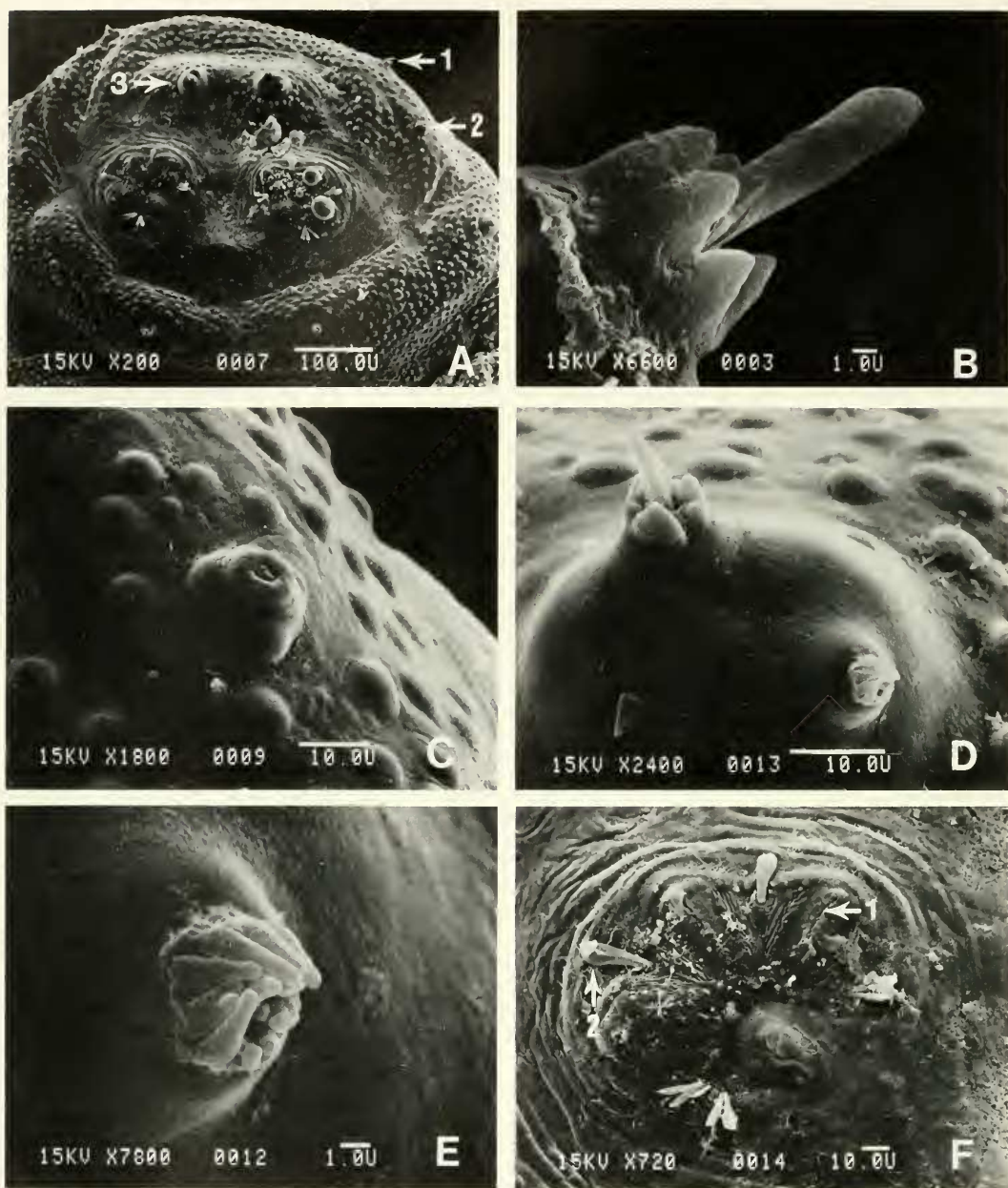


Fig. 2. Third instar larva, *Tomoplaga cressoni*, posterior end. A. Posterior view of caudal segment; 1—position of the stelex sensillum; 2—position of the domed sensillum; 3—position of the posterior sensory organ. B. Stelex sensillum. C. Domed sensillum. D. Detail of posterior sensory organ. E. Medusoid sensillum. F. Posterior spiracular plate; 1—spiracular slit; 2—lateral spiracular process.

the coniform type of sensillum (Kapoor 1986).

The posterior spiracular plates are smooth, lack verucae, and are relatively close

to the dorso-ventral midline (Fig. 2A). The rimae are elongate and flattened; the longest spiracular slit measured $25.0\ \mu$ (Fig. 2F-1). The interspiracular processes are composed

of two to four branches, the longest measuring $25.0\ \mu$ (Fig. 2F-2).

Puparium.—Fifteen puparia measured 3.8 ± 0.07 (range, 3.4–4.3) mm in length, and 1.4 ± 0.03 (range, 1.2–1.7) mm in width. The puparium is superficially smooth, bluntly rounded at the ends, and somewhat dorso-ventrally flattened (Fig. 3A). In life it is fuscous and quite distinct from the small, black, shiny puparia of its co-inhabitants, i.e. *Trupanea* spp. (see below). The anterior end is demarcated by the fracture lines which extend laterally on the first three abdominal segments. The anterior spiracles lay just dorsad of the lateral midline and bear three tubular openings (Fig. 3B-1). Closer observation revealed that the puparium surface maintained the shagreened texture of the last larval stage. The posterior end is unique among tephritid puparia examined thus far in that the sensilla were not collapsed. In other puparia such surface features are indistinguishable from the integument; however, *To. cressoni* puparia maintain erect sensilla (Fig. 3C).

DISTRIBUTION, HOSTS, AND STUDY SITES

Aczél (1955) described *To. cressoni* from specimens collected from three separate locations in interior valleys of southern California and from one location in central Arizona. Foote and Blanc (1963) added New Mexico and Texas to its distribution and mapped many collection records from coastal, interior valley, and Colorado Desert locations in southern California. Most of these California records were from bait-trap collections, which offered no clue to the host affinities of *To. cressoni*; however, Foote and Blanc (1963) also listed a U.S. National Museum record for two males reared from *Perezia microcephala* as well as sweep records from non-host *Acacia*, *Juglans*, *Solanum*, and *Solidago* spp. Aczél (1955) reported *To. cressoni* from peach, *Prunus persica* (L.) Batchelor, which Wasbauer (1972) properly termed “doubtful.” Goeden

(1987a, 1988, 1989) called attention to the often misleading nature of sweep records for adults of flower head-infesting Tephritidae.

Goeden (1983, 1987b) reported rearing *To. cressoni* from samples of flower heads of *Trixus californica* Kellogg (Asteraceae), which it infested to a limited degree along with *Trupanea conjuncta* (Adams) (Diptera: Tephritidae) and *Tru. actinobola* (Loew), both of which species were much more common in these heads (Goeden and Ricker 1989). In addition, RDG reared *To. cressoni* from samples of heads of *P. microcephala* along with *Tru. nigricornis* and *Tru. wheeleri* Curran, again, with *To. cressoni* as the least common associate. These host records from *P. microcephala* confirm rearing records for both species of *Trupanea* (Wasbauer 1972), and confirm and clarify the rearing record for *To. cressoni* in Foote and Blanc (1963). This co-occurrence of *To. cressoni* with two different species of tephritids in each of these two host plants, with only the developmental biology of *Tru. conjuncta* well known (Goeden 1987b), was one reason we did not attempt further study of its early larval stages.

Only three plant species, *Tri. californica*, *P. microcephala*, and *Hecastoleis shockleyi* Gray, comprise the Tribe Mutiseae in California (Munz and Keck 1959). This tribe is found chiefly in Mexico and South America. Thus, the two hosts now known for *To. cressoni* suggest a predictable pattern, which rearings from flower heads of *H. shockleyi* should confirm (that is, if this rare, monotypic plant species reported from the environs of Death Valley and the isolated, rugged, eastern slope of Inyo Mountain [1] can be located and [2] sampled when bearing mature flower heads!).

The principal study site with *Tri. californica* was among large, granite boulders in and above the main wash at the mouth of Chino Canyon, 1 km NW of Palm Springs, Riverside Co., during 1983–1987. *Tomoplagia cressoni* was reared from flower heads collected at this location on 25-v-1983, 7-

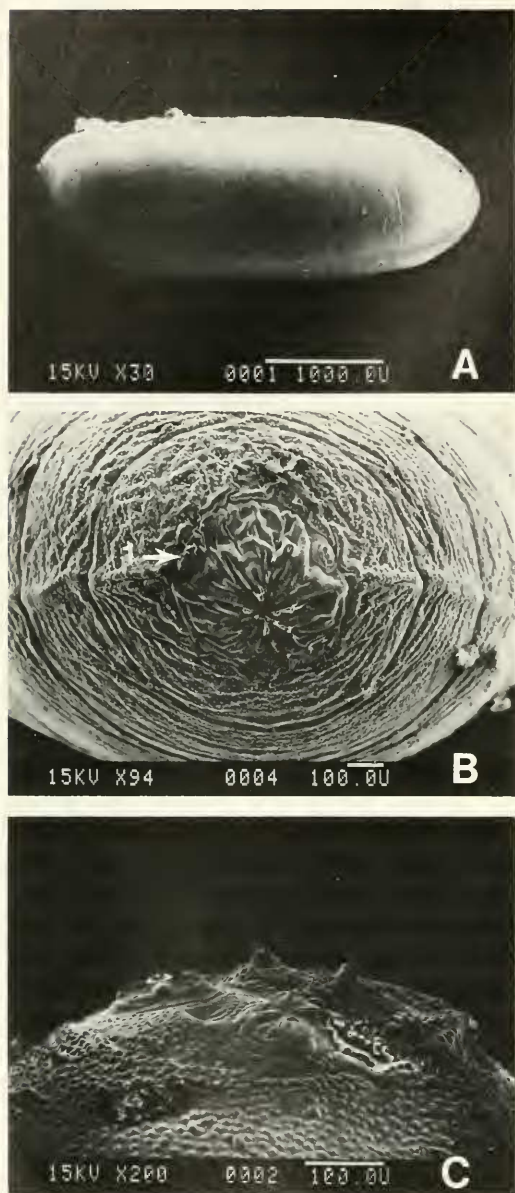


Fig. 3. Puparium of *Tomoplaga cressoni*. A. Habitus. B. Anterior end; 1—anterior thoracic spiracle. C. Posterior end, ventro-lateral view.

vi-1983, 21-vi-1983, 7-vii-1983, 1-x-1983, 15-xi-1983, 29-xi-1983, 13-iii-1984, 11-iv-1984, 24-iv-1984, and 8-v-1984. Additional locations at which flower heads of *Tri. californica* were sampled on the dates indicated, and which yielded *To. cressoni*, in-

cluded: Yaqui Pass, NE San Diego Co., 11-i-1984; Corn Spring, E Riverside Co., 12-i-1984; Desert Center, E Riverside Co., 14-iii-1984; Graham Pass, E Riverside Co., 21-iii-1984, 12-iii-1986. The only study site with *P. microcephala* was a steep, west-facing, granitic scree at the mouth of Mill Creek Canyon, San Bernardino National Forest (Northern Section), SW San Bernardino Co., during June–August, 1989.

BIOLOGY

Egg.—The eggs of *Tomoplaga cressoni* were not observed during this study, nor were gravid females swept, reared from puparia, or obtained after caging reared females (see below). Most larvae and puparia were found singly in heads of *P. microcephala* and *Tri. californica*; although, one of four infested heads examined of the latter host bore three puparia. This suggested that eggs usually are laid singly in heads.

No sign of tunneling by early-instar larvae was found in floral tubes or bracts outside of the single layer of achenes and florets that surrounded each mature larva and puparium (Fig. 4A, 4B). No oviposition punctures were noted in the outer phyllaries of infested heads. One to four, adjacent, floral tubes and ovules (this term is used to distinguish presumably unfertilized achenes in young capitula before anthesis; Harris 1990, Headrick and Goeden 1990c) from the encircling ring of florets in each head showed tunneling by an early stage larva. This suggested that eggs were inserted between or within floral tubes of immature florets by a female from an external position at the apex of a head after anthesis, and not by puncturing the phyllaries laterally with her ovipositor to gain access to the interior of a head, e.g. like *Paracantha gentilis* (Headrick and Goeden 1990b). Indeed, one sexually immature female of *To. cressoni* (determined by later dissection) was noted in a laboratory cage probing an open head with her ovipositor from such an apical position, though, of course, no egg was recovered.

Larva.—In flower heads of *Tri. californica*, the first instar of *To. cressoni* upon hatching tunnels into a floral tube, which causes the basally attached ovule to abort. The larva next transfers to and mines one or two more floral tubes. Then, and probably as a second instar, it mines one to four adjacent ovules. The larva next proceeds to score the receptacle. The third instar excavates a cuplike depression in the receptacle surface without observable tissue proliferation (no gall formation). It feeds by imbibing sap transported to the receptacle via the vascular tissues which suffuse this nurse-tissue for the developing florets (Romstöck 1987). The imbibition of sap, which collects in the feeding cavity, while concurrently scraping ever deeper with the mouth hooks into the receptacle, represents the main mode of feeding for third instars of *To. cressoni* (Fig. 4A). This feeding behavior was recently described as facultative and density-dependent among *P. gentilis* larvae in *Cirsium* thistle capitula (Headrick and Goeden 1990c), and has been found to be common, indeed obligatory (or at least consistent), even among solitary larvae of other native, flower head-infesting Tephritidae, e.g. *Neaspilota*, *Tephritis*, and *Urophora*, currently under study in southern California (Goeden, unpublished data). Three or four achenes remained intact within heads of *Tri. californica* infested by single *To. cressoni* ($n = 3$).

Larval feeding in heads of *P. microcephala* was similar to the above. First instars fed on two to four florets each, causing basally attached ovules to abort. Larvae next mined the growing ovules, then tapped into the receptacle and became primarily sap feeders, at least as third instars. The larvae always fed at the peripheries of the receptacles in heads of *P. microcephala*. Larvae were located between the inner phyllaries and several, contiguous, undamaged developing achenes oriented with their long axes parallel to these flower head parts (Fig. 4A). An average of 6 ± 0.7 (range, 0–10) achenes

remained undamaged in 13 heads that contained one mature larva or puparium each of *To. cressoni*. Uninfested heads contained an average of 11 ± 0.1 (range, 9–13, $n = 77$) achenes. *To. cressoni* directly and indirectly destroyed less than half of the achenes in heads it infested. Flower heads of *P. microcephala* which contained one puparium each of *To. cressoni* and either *Tru. nigricornis* or *Tru. wheeleri* yielded adults of both species.

Schwitzgebel and Wilbur (1943) reported that *To. obliqua* (Say) was reared from seeds of ironweed, *Vernonia interior* Small, in Kansas. F_1 larvae reportedly fed on the ovules; F_2 larvae, on “seeds,” presumably meaning achenes, and destroyed all seeds in a head. In ironweed, *To. obliqua* co-infested heads with *Neaspilota alba* Loew, in which the former tephritid also was the subordinate or much less common associate.

Pupa.—When feeding was completed in heads of *P. microcephala*, the larva reversed itself 180° and pupariated with its posterior end cupped and lightly glued, probably by dried sap, within its feeding cavity in the receptacle (Fig. 4B). Empty puparia in excised, dry, open heads of *Tri. californica* that had been held for adult emergence in sleeve cages, on the other hand, had been lifted off the receptacles and were lightly glued among pappus hairs.

Adults.—Adults (Fig. 4C) pushed upward and outward through the pappus in exiting the flower heads, as described and illustrated for *P. gentilis* by Headrick and Goeden (1990b). A total of only 13 males and 11 females emerged from 11 of 33 weekly or biweekly samples of flower heads of *Tri. californica* collected between May 1983 and May 1984 at Chino Canyon. A total of 27 males and 29 females was recovered from three biweekly samples of heads of *P. microcephala* in 1989. These data indicated an equal sex ratio for *To. cressoni*.

Dissections of newly emerged females determined that they are sexually immature ($n = 3$), and that neither sex contained much

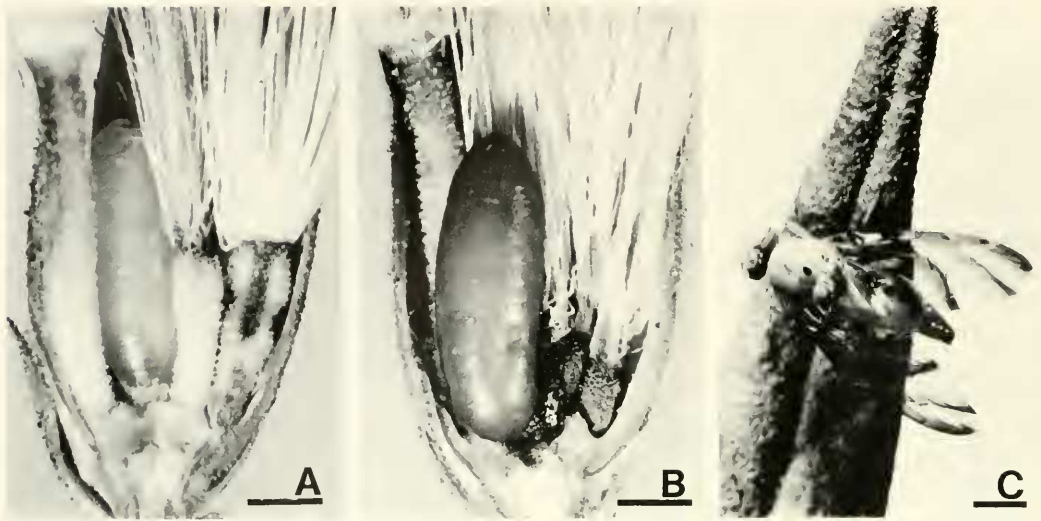


Fig. 4. Life stages of *To. cressoni*. A. Third instar larva in flowerhead of *P. microcephala*. B. Puparium in flowerhead of *P. microcephala*. C. Adult female on leaf of *Tri. californica*. Bars = 1 mm.

fat body tissue. Newly emerged adults of *P. gentilis* (Headrick and Goeden 1990b) and all species of *Trupanea* studied in southern California to date (Cavender and Goeden 1982, Goeden 1987b, 1988, and unpublished data) are sexually immature and contain little fat body tissue, unlike some newly emerged gall-formers, e.g. *Eutreta diana* (Osten Sacken) (Goeden 1990). Furthermore, although eight females lived an average of 118 ± 11.3 (range, 67 to 152) days, and 11 males, 78 ± 9.6 (range, 31 to 126) days in individual plastic cages supplied with honey and water, as described by Goeden and Headrick (1990), they remained sexually immature.

Only one of 13, 2-day-long pairings of these virginal flies between the ages of 2 to 109 days resulted in mating. Plastic petri dishes were used as arenas for mating tests (after Jenkins 1990), which we modified for longer use by including a pad of absorbent cotton saturated with distilled water and spotted with drops of honey. A 94-day-old male and a 105-day-old female (both virgins) were first observed *in copula* after dusk under artificial light at 18:24 h PST on 30

Oct 1989. Courtship by these flies had not been observed; however, this behavior had been seen earlier with one each, 28–30 and 58–60 days-old virginal males in separate pairings. These courting males had laterally ballooned abdominal pleura, and both actively pursued the same-aged females with which they were caged. Alternatively, these males stood still, faced, and fanned their wings synchronously towards the females, but, again, no mating resulted. The ballooned abdominal pleura of *To. cressoni* males appeared as photographed with *Tru. bisetosa* (Cavender and Goeden 1982). Ballooned males abdominal pleura have now been reported from several genera of non-frugivorous as well as frugivorous Tephritidae, and are thought to be involved in pheromone dissemination (Jenkins 1990, Headrick and Goeden 1990b).

The copulatory position of *To. cressoni* differs from postures described for other mating, nonfrugivorous tephritids. The ovipositor is held straight backward, not curved upward during copulation, which requires that the male ride more posteriorly and upright, i.e. nearly perpendicular to the sub-

strate. Also, during the early stages of the single, but protracted mating observed, the female extended her ovipositor to nearly its full length, then retracted it, moving it in and out in a rhythmic manner while joined to the male. Accordingly, the abdomen of the male moved forward and backward through an arc of 30 to 40°. This pumping activity gradually ceased as mating continued. The foretarsi of the male grasped the middle of the abdomen of the female dorsolaterally, his midtarsi grasped the base of her oviscape, and his hind tarsi rested on the substrate. The wings of both sexes were held motionless and parallel to the substrate. The female's wings were parted about 45° from her midline, and the male's wings, about 30° from his midline. The mouthparts of both sexes pumped rapidly (five to six pumps/sec.) during mating. This mating lasted at least 3.5 h and was discontinued within 5 h after the lights had been turned off.

Other behaviors that distinguish *To. cressoni* adults involved resting and walking. The usual resting postures of both sexes were with their wings held outward about 80° from their bodies, or sometimes at lesser angles. The costal margin is curled forward, i.e. supination (Headrick and Goeden 1990b). As the adults walked forwards, they synchronously brought their wings upward and forward, then downwards and backward, the long axes of both wings moving together in ellipses. This wing movement appears much like the butterfly stroke of human swimmers. This movement is distinct from the agonistic wing thrusts described for females of *Aciurina mexicana* by Jenkins (1990) and others. Two- and 10-day-old, virgin females of *To. cressoni* repeatedly signaled their nonreceptiveness to same-aged males, in arenas, by rapidly rushing towards them with their wings extended forwards, costal surfaces downward and ventral surfaces anteriorad. One 10-day-old male displayed similar agonistic behavior towards the same-aged female with which

he was caged. The onrushing females and male came close to the other flies, but always avoided touching by stopping or turning.

Seasonal history.—*Tomoplagia cressoni* has at least two, sometimes three, annual generations in southern California: one on *Tri. californica* in the low-elevation Colorado Desert each spring, another produced on its alternate host, *P. microcephala*, in interior valley foothills in the summer, and under certain conditions, a third generation produced on *Tri. californica* in the fall. The long-lived adults may migrate to bridge the time intervals and distances separating flowering populations of these two hosts. How and if, the third potential host plant, *H. shockleyi*, fits into this scheme has yet to be determined. During and following the exceptionally wet winter of 1982–83, *Tri. californica* flowering and *To. cressoni* emergence were extended well into the summer (July) at Chino Canyon. A second flush of flowerheads and a second generation of *To. cressoni* were produced at Chino Canyon in October and November, 1983, in response to late-summer rainfall. However, with no fall rainfall, only one crop of flower heads and the spring generation of flies were produced at Chino Canyon in 1984. Apparently, *To. cressoni* usually infests the earliest and latest flower heads, but has little success competing with *Tru. actinobola* and *Tru. conjuncta* for the bulk of the flower heads produced by *Tri. californica* (Goeden 1987, Goeden and Ricker 1989).

Mortality factors.—Some of the parasitoids and predators of *Tru. conjuncta* reported by Goeden (1987) probably also attack *To. cressoni* as well as *Tru. actinobola* in flowerheads of *Tri. californica*. One male and one female *Eurytoma veronia* Bugbee (Hymenoptera: Eurytomidae) were reared as primary, solitary, larval-pupal endoparasitoids of *To. cressoni*, and at least *Tru. wheeleri*, in heads of *P. microcephala*. Similarly, one female each of *Colotrechnus ignotus* Burks (Hymenoptera: Pteromalidae)

was reared as a solitary parasitoid from a puparium of *To. cressoni* and a larva of either *Tru. nigricornis* or *wheeleri* in heads of *P. microcephala*. Finally, a female *Pteromalus* sp. (Hymenoptera: Pteromalidae) was reared as a primary solitary parasitoid of *To. cressoni*. These parasitoids were reared from isolated parasitized hosts in a humidity chamber (76% R.H.).

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